J. Exp. Biol. (1968), 49, 285–297
With 10 *text-figures*
Printed in Great Britain

EYECUP WITHDRAWAL IN THE CRAB, *CARCINUS*, AND ITS INTERACTION WITH THE OPTOKINETIC RESPONSE

BY M. BURROWS* AND G. A. HORRIDGE
Gatty Marine Laboratory and Department of Natural History, University of St Andrews, Fife, Scotland

(*Received* 19 *February* 1968)

INTRODUCTION

A strong stimulus to cuticular receptors on or around the eyes causes a rapid withdrawal or retraction of the eyecup in many decapod Crustacea. In many crabs, such as *Carcinus*, the eyecup flicks back into its socket by a movement away from the mid line, but it must be remembered that in other decapod crustaceans eyecup retraction is toward the mid line. Optokinetic or geotactic eyecup responses which may be going on at the same time as a withdrawal are temporarily discontinued. Something is already known of the electrophysiology of this response. Section of the optic tract abolishes the rapid withdrawal, but the eyecup can still be withdrawn slowly and can be held in the retracted position. After section of the oculomotor nerve the eyecup can retract quickly but cannot be held in the withdrawn position. Therefore some, at least, of the fast motoneurones run in the optic tract and some of the slow ones in the oculomotor nerve (Sandeman, 1964; Horridge & Sandeman, 1964).

The withdrawal response is unilateral and is most easily evoked by mechanical stimulation of an area of carapace supplied by the tegumentary nerve (Bethe, 1897), although direct electrical stimulation of ipsilateral brain nerves is effective (Sandeman, 1967). A high-frequency train of large impulses with individual units approaching a frequency of 500 Hz. is easily recorded from the optic tract and is correlated with the withdrawal movement, but is not modified if the eyecup is restrained or even removed altogether (Horridge & Sandeman, 1964). This paper is concerned with the action of the eyecup muscles which bring about withdrawal, and the effect on the visual input of eliciting this reflex. A preliminary report of some aspects has appeared (Burrows, 1967).

METHODS

The same recording methods were used as in previous work. Extracellular and intracellular microelectrodes were implanted in eyecup muscles by the methods described by Burrows & Horridge (1968*a*). Movements of the eyecup and of a brightly illuminated striped drum were each recorded separately by the shadow cast by a black paper flag over a photocell, as described by Horridge (1966*a*). A larger photocell than that previously employed, of length 2 cm. and width 3 mm., was necessary to record the total movement of the eyecup. In some experiments the movements of the two eyecups were recorded simultaneously, together with the actual drum movement, and the results were displayed on a multiple-channel pen recorder.

* Present address: Department of Biology, University of Oregon, Eugene, Oregon 97403, U.S.A.

RESULTS

Eyecup withdrawal

Protective withdrawal

A stimulus to any point around the eyecup causes it to withdraw. The response is easily repeatable and remarkably consistent. A survey of the eyecup muscles with intracellular electrodes in a clamped eye, and extracellular electrodes in a freely moving eye during the withdrawal response, reveals the following.

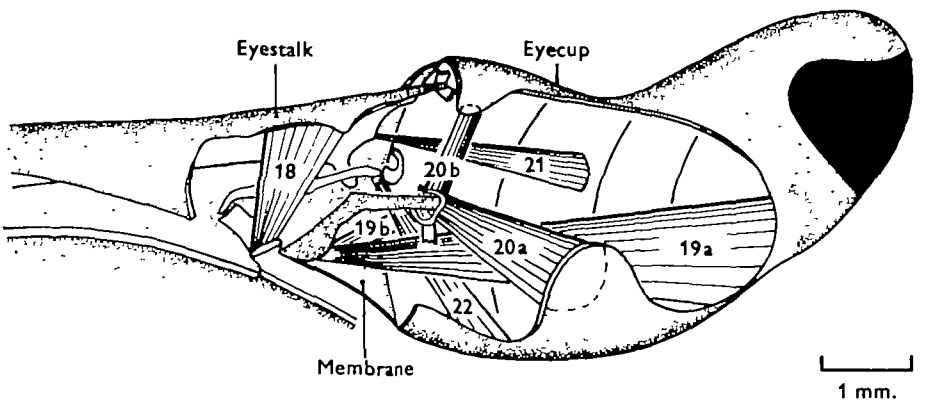

Fig. 1. Muscles involved in the withdrawal of the right eyecup, seen from the lateral side. Other muscles (20c, 23a and 23b) are not shown. The eyecup muscles suspend the eyecup upon a joint which can bend in all directions. Muscle 18 rotates the eyestalk relative to the main body skeleton. The withdrawal movement is downwards and laterally, i.e. out of the page in this figure.

The stimulus causes two separate trains of spikes to emerge from the brain in two motoneurones of the optic tract. No matter how the recording conditions on the optic tract are changed, or how the preparation is fatigued by repeated excitation, only two motoneurones are active. The muscles innervated by these two neurones are shown in Fig. 1. The spikes of larger amplitude in the optic tract are correlated with junction potentials recorded simultaneously in muscle 19a and never in muscle 18, while the smaller spikes are correlated with the junction potentials in eyestalk muscle 18 (Fig. 2A, B) and never in 19a. These two axons also travel to other eyecup muscles, as is revealed by exploration with two electrodes in different muscles. Junction potentials in muscle 19a correspond with those in some fibres of muscle 19b and with those in a small number of fibres on the dorso-lateral surface of muscle 20a (Fig. 2C, D). Similarly junction potentials in muscle 18 correspond to those in some fibres in muscles 20b, 21 and 22 (Fig. 2F, G, H). Phasic activity correlated with eyecup withdrawal has not been found in the three remaining eyecup muscles, 20c, 23a and 23b, and in fact the two latter are active during eyecup extension.

Two axons and seven muscles are clearly involved in the protective withdrawal; the axon with the large-amplitude spike innervates three muscles, 19a, 19b and 20a, while the axon with the smaller spike innervates a group of four, 18, 20b, 21 and 22. A latency of 10–20 msec. between stimulation of the tegumentary nerve and the appearance of the first junction potential is the same for both muscle groups, but their responses are different. The junction potentials in muscles 19a, 19b and 20a facilitate

and summate rapidly, with graded spike-like responses which sometimes overshoot zero membrane potential. This series of impulses lasts for 50–500 msec., depending on the preparation. The response in the second muscle group occurs at a lower frequency and is longer lasting. The junction potentials facilitate and summate but there are no active membrane events.

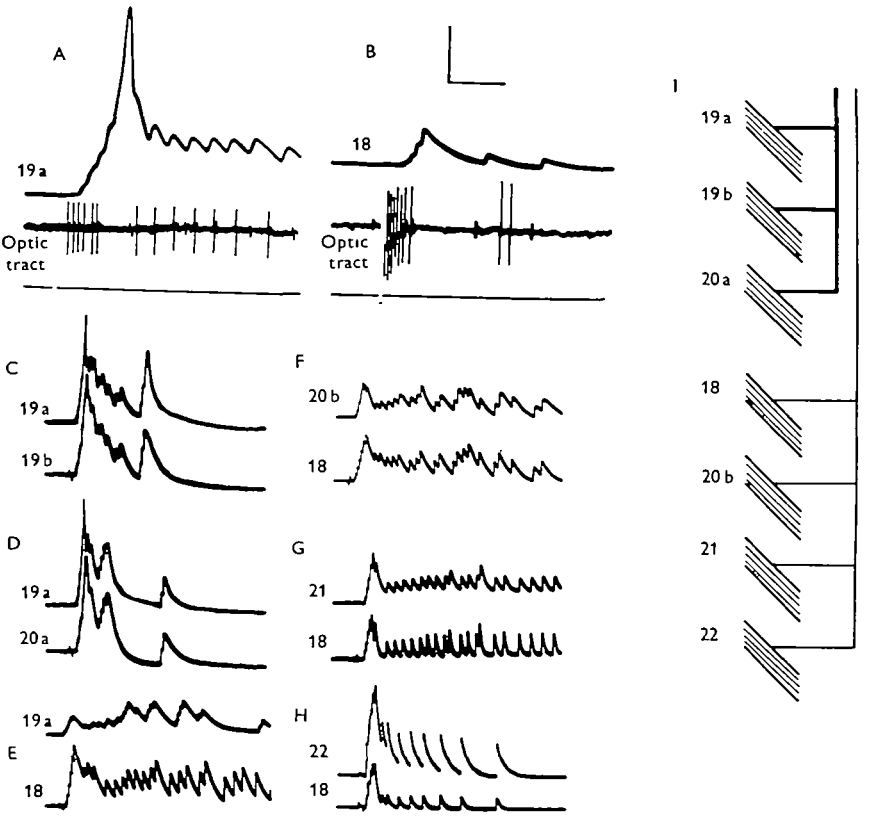

Fig. 2. Reflex eyecup withdrawal. A and B, activity simultaneously recorded from two motoneurones in the optic tract and in muscle 19a (A) and muscle 18 (B), in response to a single shock applied to the tegumentary nerve. Junction potentials in 19a are in phase with the large spikes and those of 18 with the small ones. C–H, other peripheral connexions of the same motoneurones are revealed by the occurrence of some simultaneous and some independent junction potentials in intracellular recordings from pairs of muscles. I, the inferred connexions to all the muscles involved. Scale: A and B, 20 mV., 40 msec.; C–H, 40 mV., 200 msec.

Muscle 19a is the only muscle from which no electrical activity is recorded during optokinetic or geotactic responses. Compared to the other eyecup muscles it is histologically remarkably uniform in that all fibres have a resting sarcomere length of 3–4 μm. When two different fibres are penetrated in muscle 19a during a withdrawal they show synchronized phasic responses, but may differ in that some are more strongly innervated by a slow axon which runs in the oculomotor nerve. In an unrestrained eyecup the tonic activity at a frequency of 30–40 Hz. caused by this slow axon occurs only when the animal actively holds its eyecup in the withdrawn position. Every detail of innervation agrees with the previous finding that the maintenance of

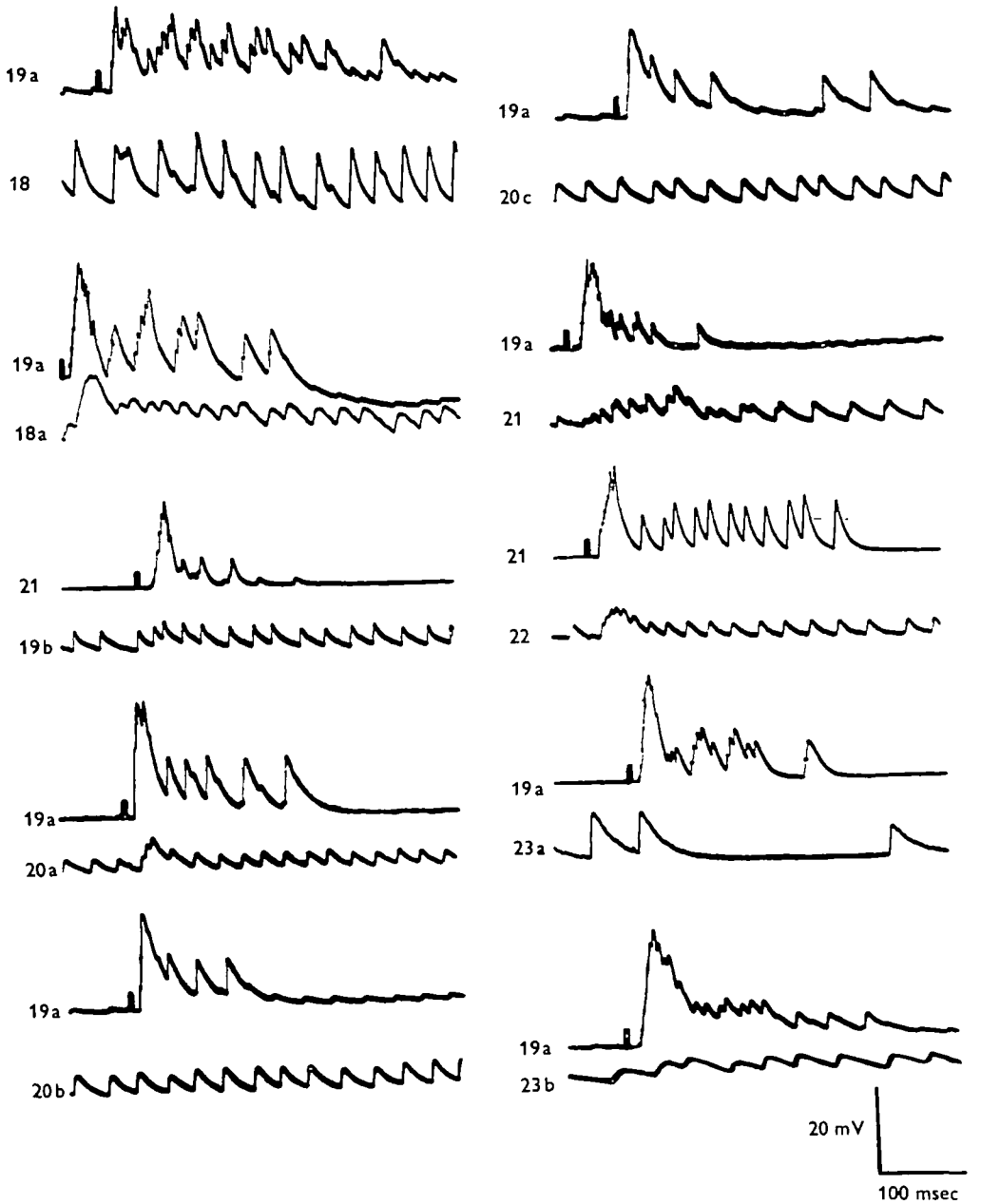

Fig. 3. The effect of reflex withdrawal on tonic activity in various muscles. Tonic activity in muscles 19b and 22 is recorded with phasic withdrawal activity in muscle 21, while that in the remaining muscles is recorded with muscle 19a. No activity is inhibited peripherally and only that in muscle 23a is inhibited centrally; the remainder is overridden mechanically. In addition to the fast fibre which they all have, the various fibres of muscle 19a show different densities of innervation by a slow axon that is responsible for holding the eyecup in its socket once withdrawn.

withdrawal depends on motoneurones that emerge in the oculomotor nerve, while the fast withdrawal movement depends on axons of the optic tract (Sandeman, 1964).

In muscles 19b, 20a, 21 and 22 only those fibres that respond phasically in optokinetic movements are innervated by the fast withdrawal axons, but in muscles 18 and 20b some tonic fibres are also excited. There is no unequivocal evidence that any fibres in these muscles are innervated solely by the withdrawal axons, as they are in 19a. All fibres penetrated in these muscles responded in optokinetic or geotactic reflexes, or in both, as well as in withdrawal.

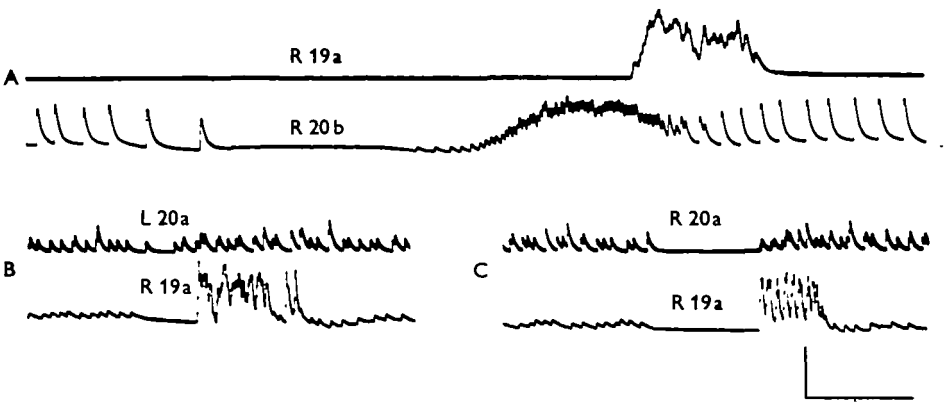

Fig. 4. 'Spontaneous' eyecup withdrawal. A, recordings from muscles 19a and 20b during a 'spontaneous' withdrawal showing a period of central inhibition which precedes withdrawal and the burst of activity in muscles 20b and 19a which causes withdrawal. B, contralateral tonic activity (L 20a in B) is slightly slowed during a 'spontaneous' withdrawal of the ipsilateral eyecup, while that in the ipsilateral eyecup itself (R 20a in C) is completely inhibited. Scale: voltage 20 mV.; time in A, 250 msec.; B and C, 500 msec.

The tonic activity which normally locates the eyecup in space is surprisingly little modified during a reflex withdrawal. None of the motor activity is inhibited peripherally and only that in muscle 23a is inhibited centrally (Fig. 3). Therefore tensions in the muscle fibres which control eyecup position under visual and geotactic reflexes are overridden by the stronger contraction of the fibres activated by the withdrawal axons. After withdrawal of the eyecup the oculomotor activity continues as before regardless of whether the eyecup is extended or retained in its socket. At the relaxation after a reflex withdrawal the eyecup recovers its former position principally because of this persistence of the balance of tensions in the eyecup muscles.

Spontaneous withdrawal

In a normal crab there are spontaneous withdrawals of the eyecup at irregular long intervals. When one statocyst is removed in a crab whose other sensory input is kept constant, the withdrawals of the ipsilateral eyecup speed up, to intervals of 10–50 sec. (Sandeman, 1967). This 'spontaneity' indicates some kind of iterative mechanism in the brain which is normally inhibited by the action of the statocyst. The execution of the spontaneous withdrawal is quite different from that of a reflexly evoked one. Up to ½ sec. before a spontaneous withdrawal the tonic activity in all the eyecup muscles is inhibited centrally and there is even a slight slowing of the tonic activity in the contra-

lateral eyecup (Fig. 4). There is therefore some central interaction between the two sides although the behavioural output is superficially restricted to one eye. Following the inhibitory period, junction potentials are recorded in muscles 18, 20b, 21 and 22, which are the group supplied by the axon with the small spike. These junction potentials increase in frequency, summate, and also facilitate slightly to reach a depolarization plateau which may last for up to 500 msec. During this plateau a high-frequency burst of rapidly facilitating and summating junction potentials with some active responses occurs in muscles 19a, 19b and 20a, the group supplied by the axon with the large spike (Fig. 4). Although this is the normal firing pattern, the phase relation between the two retraction axons is somewhat labile and in some preparations activity in the two axons may be completely dissociated. Spontaneous firing in one or other of these axons could account for the variety of directions of small saccades or flicks of the eyecup, many of which appear to be incipient spontaneous withdrawals, because impulses in the axon supplying muscles 18, 20b, 21 and 22 cause a movement upward and toward the mid line, while impulses in the other axon cause a movement away from the mid line and downward. When both axons fire a burst together the movement is a withdrawal because the stronger pull, mainly exerted by muscle 19a, is in that direction.

Each mechanism of withdrawal is the consequence of a central programme of efferent impulses which is not dependent on the subsequent eyecup movement, or even on its presence. The same pattern of motor impulses is recorded whether the eyecup is freely moving or whether it is clamped in any abnormal position.

Eyecup extension

The extension of the eyecup after a reflex or spontaneous withdrawal returns it to the position which it formerly occupied. Records of the freely moving eyecup show

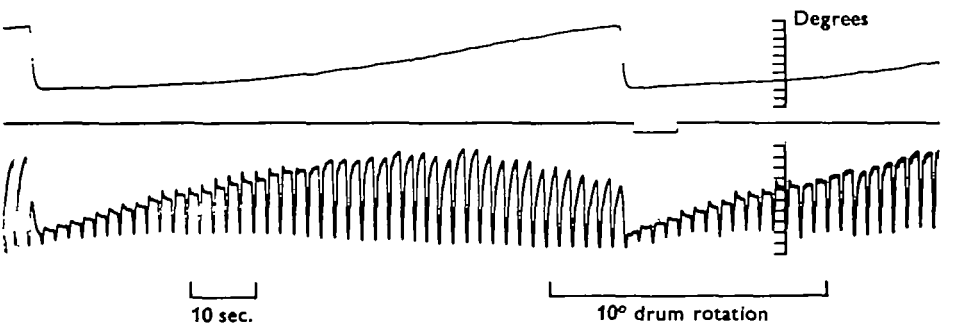

Fig. 5. Simultaneous records of positions of right (upper trace) and left (lower trace) seeing eyes in response to drum movement towards the left of the crab. Shocks applied to the region of the left eyecup cause it alone to withdraw at each shock; the right eyecup is unaffected. The record shows that relaxation each time is to the point previously reached by the eyecup. At higher frequencies of stimulation there is a greater maintained withdrawal of the eyecup.

that the return to the previous position is precise, and that the eye returns to a position which is actively maintained, not just to a central point determined by elastic recovery. This is shown by the extension after a spontaneous or after a reflex withdrawal which occurs during a horizontal optokinetic response to the movement of a striped drum

(Fig. 5). The return of the eyecup to the position which it had previously reached under the influence of the drum is a controlled movement, which slows progressively as it comes to its final position and does not suggest in any way that the eye springs out just because the phasic and tonic withdrawal activity suddenly terminates. Characteristic changes in frequency, which are sawtooth in form and which correspond exactly with the horizontal movements of the eye, are recorded from tonic fibres of either muscle 20a or 21 during optokinetic nystagmus (Fig. 6). Each muscle pulls the eyecup towards its own side as the frequency in its tonic fibres progressively rises. At the end of the slow forward phase there is a sudden fall to the low frequency found at the beginning of the traverse.

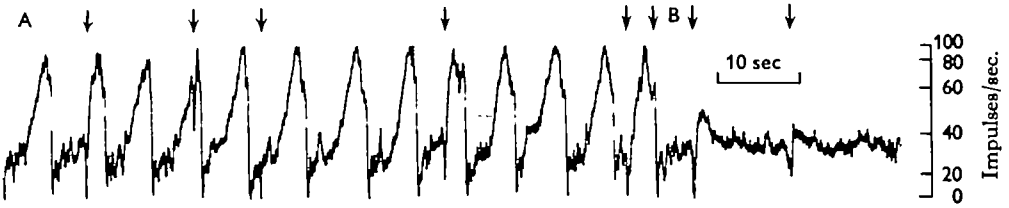

Fig. 6. A, a pen record of the frequency of tonic impulses in muscle R 21 (which pulls the eye towards the mid line) with a continuously moving drum as stimulus. The eye is blind and is driven by visual stimulation of the other eye. The frequency rises as the slow forward phase of nystagmus progresses and drops to zero at each fast return phase of the response. Spontaneous withdrawals (arrows) are marked by a temporary drop in the frequency, followed by an immediate return to the previous level. B, the drum movement is stopped and a continuing visual excitation is shown by an increase in frequency to a steady level of about 40 Hz. The two further spontaneous withdrawals with the drum stationary have only a temporary effect on tonic impulse frequency.

A spontaneous eyecup withdrawal during one of these records is apparent as a brief fall in frequency *followed by immediate recovery to the appropriate value* (Fig. 6). This result is found whether the eye which withdraws spontaneously is blind and driven by the visual input to the other eye, as in Fig. 6, whether both eyes see or whether the eye which withdraws is the only eye which sees. Therefore a continuing visual input from the eye which does not withdraw is not essential for the maintenance of the tonic frequency which would hold the eyecup in position. There must be some kind of central memory which stores temporarily the values of the tonic frequencies to these eyecup muscles.

Attainment of the former eyecup position therefore depends on two forms of recovery after withdrawal: (*a*) eye muscles maintain their background tension but are overridden briefly by the tensions superimposed by the discharge of the two withdrawal motoneurones (this happens in reflex eyecup withdrawal); (*b*) motor axons are centrally inhibited for a brief period but removal of the inhibition leaves the previous excitatory state unchanged so that the impulse frequency is resumed as it was before (this is characteristic of spontaneous eyecup withdrawal).

A separate mechanism of eyecup extension can be recorded from muscles 23a and 23b, on the dorsal surface of the eyecup, which give bursts of junction potentials of slowly rising frequency when the eyecup extends. These bursts are frequently complete before the eyecup has recovered its position so they do not complete the extension, although they appear to start off the movement. The point of interest is that the

size of this burst of potentials at extension is linked to the strength of the previous withdrawal (Fig. 7). This fine control is not the result of proprioceptive monitoring of the eyecup position because similar patterns of impulses are obtained when movement is prevented. In the experiment shown in Fig. 7 the eye started from the same position each time, with successive withdrawals taking the eye farther into the socket, and we have no evidence that the extension response depends on the position from which the eye started its withdrawal. Although muscles 23a and 23b contribute in a graded way in the extension of the eyecup, their apparent role is to lift the eye quickly from its socket, whereupon the continuing tonic activity returns it to its former position.

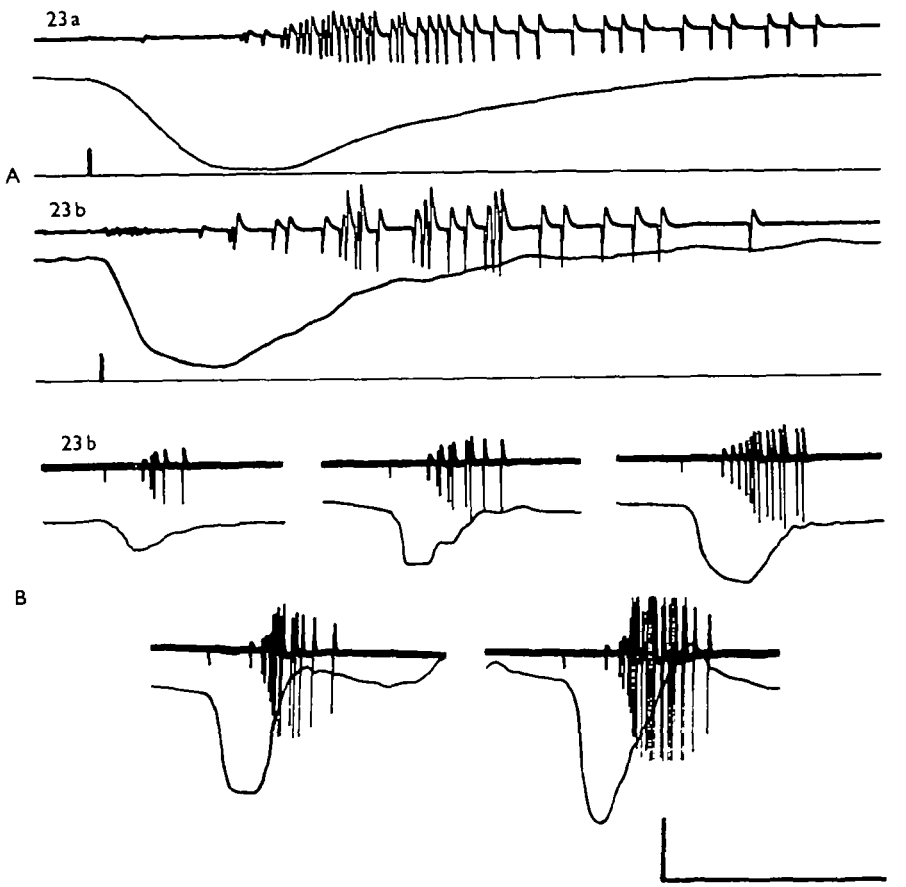

Fig. 7. Eyecup extension. A, the eyecup has been induced to withdraw by a light touch to the carapace (lower traces) and extracellular muscle potentials are recorded from muscles 23a and 23b (upper trace in each record) together with the resulting extension movement of the unrestrained eyecup (middle traces). Records are from different crabs. B, successive withdrawals of increasing amplitude are induced by increased mechanical stimulation of the carapace. Eyecup movement is recorded together with activity in 23b (upper trace). Activity in the extensor muscles is directly linked to the amplitude of the withdrawal. Scales: voltage 1 mV.; eyecup movement 10°; time in A 300 msec., in B 1 sec.

Interactions involving the withdrawal response

Withdrawal reduces the optokinetic response

It was mentioned above that a withdrawal movement is superficially independent on the two sides of the crab. This is true for spontaneous and brief reflex withdrawals. However, repeated shocks to the region around one eyecup can reduce the optokinetic response of the other eyecup when the shocks are applied to the eyecup which is moving towards the mid line of the crab. The effect is shown in Fig. 8. The right eye, moving in slow phases towards the mid line, is stimulated at 1 Hz. with shocks applied to the right antennule, which is a convenient point for this purpose. Although both eyes are free to move and see, the left eye stops for a while in its path. The left eye sees and its movement is smooth; therefore its failure to respond is not entirely due to the jerky movement of the right eye which repeatedly retracts.

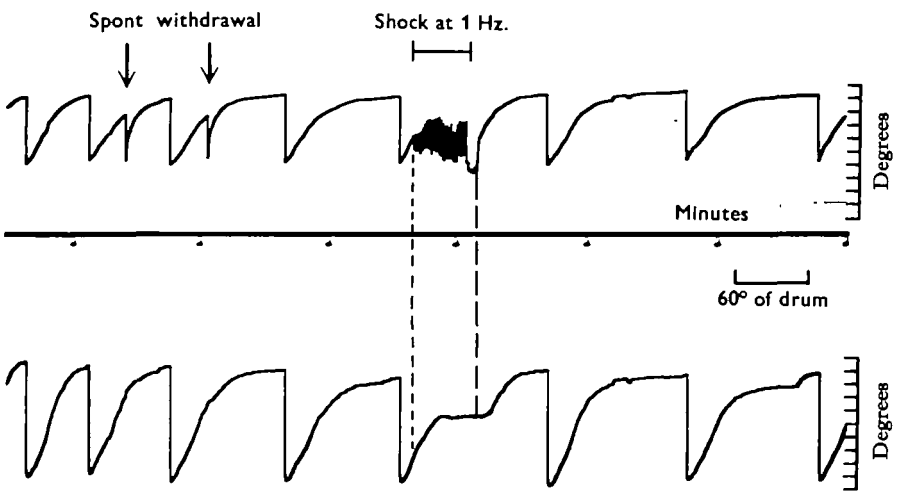

Fig. 8. Simultaneous movements of the right (upper trace) and left eye (lower trace) as the drum moves towards the mid line for the right eye. Spontaneous retractions, shown by the arrows, have no observable effect on the movement of the other eye. Reflex withdrawals of the right eye at 1 Hz. (horizontal line) inhibit the response of the left eye. Note the 10 sec. latency of the effect on the left eye.

The inhibitory effect is transmitted from the right side to the left with a latency of several seconds, as shown by the continued smooth movement of the left eye for some time after the right eyecup is stimulated. Similarly the left eyecup does not begin to move forward again until some seconds after the end of the stimulation to the right side. This eliminates the abnormal movement of the right eyecup as a cause of the inhibition of the left.

This effect is consistent so long as the direction of the visual movement is maintained constant in relation to the side which receives shocks. Similar stimulation of an eyecup moving away from the mid line fails to show the effect.

Arousal of the optokinetic response by stimulation

In the above experiments tests with shocks so weak that they induced no withdrawal at all had quite a different effect in increasing the optokinetic response. Possibly a different class of cutaneous receptor fibre is excited, but, whatever the mechanism, it is clear that the typical response of the eyecups is not the best that the crab can do.

The most convenient visual stimulus is a regular sinusoidal oscillation of a vertically striped drum. After some minutes of oscillation the response of the eyecups falls to a steady value. At low frequencies the eyecup generally oscillates through an angle about half that of the amplitude of the drum's movement. When only one eyecup has vision and drives the movement of the other (which is blinded by black paint on the cornea) the blind eye commonly follows the stimulus less effectively than the seeing eye, especially after a long period of stimulation.

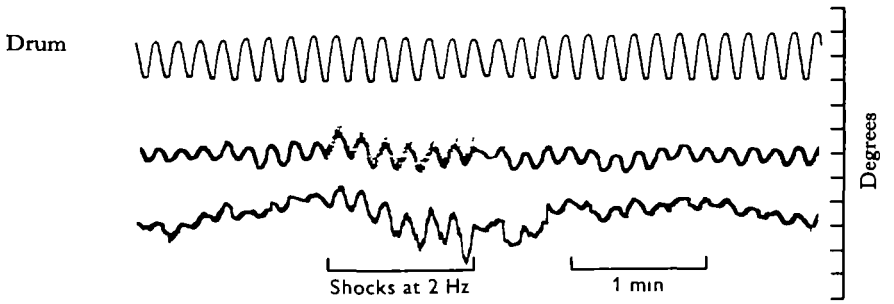

Fig. 9. Improved response of the blind and driven left eye (lower trace) when the area innervated by the tegumentary nerve on the right side is given weak shocks at 2 Hz. There is little increase in the oscillations of the right seeing eye (upper trace) in this example. The top line shows the oscillationof the drum.

Weak stimulation to the integument or the antennule on the side of the seeing eye brings back the response to the visual stimulus (Fig. 9). Usually the response is more marked in the blind eye because its performance was previously so poor. When the stimulus is very weak the effect lasts only as long as the stimulus is applied.

Arousal of the optokinetic response by eyecup withdrawal

Acting perhaps in the same way as weak stimulation, the movement of the eyecup during a withdrawal causes an enhancement of the optokinetic response. The effect is most apparent when the eye spontaneously retracts while the drum is continually moved sinusoidally at low frequency. The effect is similar if the withdrawal is reflex. In tests of arousal in the two different situations the response after the brief spontaneous withdrawal is in addition to the enhancement which has been brought about by mild electrical stimulation (Fig. 10A). An eyecup which is in process of extension typically responds about twice as well to drum oscillations as it did when fully extended. The remarkable fact, to be dealt with in a succeeding paper, is that the animal fails to respond to the stimulus that is caused by its own movement in extending across the pattern of the drum.

When a seeing eye retracts and slowly extends again, the enhancement of the response to oscillation does not necessarily influence the movement of the other eye if it is blind and driven by the opposite seeing eye (Fig. 10B). Similarly if the blind driven

eye is caused to retract, or is stimulated mechanically by 'wiggling' it on its joint, an enhancement of the response is not seen in the movement of the seeing eye. Therefore this effect has the appearance more of a unilateral improvement of the motor response than of an improvement in the movement-perception system of the seeing eye.

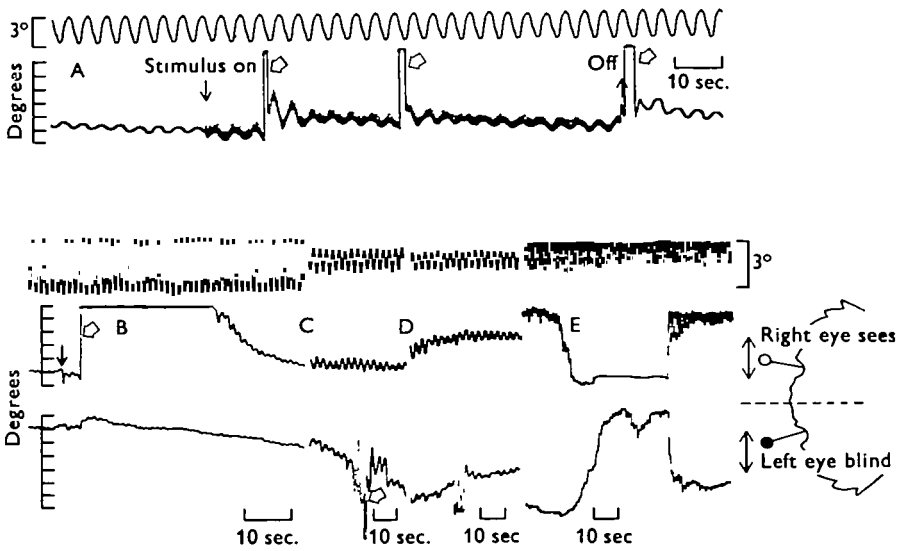

Fig. 10. Arousal of the optokinetic response. A, shocks at 2 Hz. (arrows) to the region innervated by the tegumentary nerve on the side of the seeing eye cause a slightly increased response to the regular drum oscillations. There is a further increase in the response immediately after each spontaneous retraction (open arrows) whether the electrical stimulation is continued or not. B, a touch to the seeing eye (upper trace) causes an improved response of the driven blind eye (lower trace). The seeing eye then retracts spontaneously (open arrow), and the improved response during extension and the slow sweep across the drum are not conveyed to the left eye. C, the blind eye is moved forcibly, which leads to its retraction (open arrow). The increased response of the blind eye during its extension is not conveyed to the seeing eye. D, 'wiggling' the blind eye in any plane has no effect on the response of the seeing eye. E, the seeing eye is forcibly pushed toward the mid line, which results in a convergent movement of the blind eye, and then released. The response of the seeing eye is improved.

The eye sees when withdrawn

In the normal withdrawn position of the eyecup only about half of the cornea is covered. The remainder sees out from the shelter of the eye socket. In this position it will still drive the movements of the other eye when that is blinded (Fig. 10B). Therefore movement perception persists; this is true whether the eye is actively withdrawn and held in firmly by the crab, or whether it is pushed in artificially by the experimenter.

If an eye is prodded with a pencil it withdraws quickly and stays withdrawn while the pencil hovers near, even when the other eye is covered. This is sufficient to illustrate the value of continued vision while the eyecup is withdrawn.

Stimulation of eyecup extension

The most effective way of persuading a crab to extend its eyes if they are withdrawn is to excite mechanoreceptors anywhere on the body outside the area supplied by the tegumentary, antennular and antennal nerves. Tickling the legs or the abdomen is the

method of choice: pouring sea water over the mouth is often effective. Although it has not been strictly worked out, the most effective stimulus is on the same side of the body as the eye to be extended. Ascending interneurones to the motor centres in the brain must be involved.

Quite a different type of modification of the optokinetic response occurs under the same circumstances. When crabs with extended eyecups are tickled as above there is a marked arousal of the optokinetic response (Horridge, 1966*b*). This arousal is possibly mediated by ascending mechanoreceptor interneurones which run to the optic lobes but are excited by thoracic and abdominal stimulation (Bush, Waterman & Wiersma, 1964).

DISCUSSION

The outstanding feature of reflex retraction of the eyecup is that it is not co-ordinated with other movements going on at the same time; it simply overrides everything else. Tonic motor impulses to the eight eyecup muscles that are involved in maintaining a desired eyecup position persist at frequencies which are set by the sensory input from the statocyst and by the recent history of movement in the visual field. After a withdrawal the eyecup may then be retained within its socket, by the action of a slow-motoneurone discharge to muscle 19a, although still able to see. Relaxation of 19a tonic activity is essential for the eyecup to extend again. Extension is brought about by bursts of activity in muscles 23a and 23b. Their function is to lift the eyecup quickly from its socket, while recovery of the position before the withdrawal is determined by the maintained tonic activity in eight of the nine eyecup muscles. During a spontaneous withdrawal all tonic activity is temporarily inhibited centrally.

The fine control of the recovery of eye position lies in the mechanism which sets the motor impulse frequency to the tonic eye muscles. The interesting feature of the central mechanism is its ability to maintain the impulse frequency of the appropriate motoneurones over the period of a withdrawal. For this to happen there must be a persistence of movement seen or inferred since the crab last made a fast phase in optokinetic nystagmus. Any movement of all contrasts in the visual field modifies the central programme of tonic motor impulses to eight eye muscles. The changed programme is then maintained for periods of minutes if there is no further perception of movement. Evidently the temporary central inhibition of the motoneurones during a spontaneous withdrawal does not prevent this persistence.

As for other eyecup reflexes, the impulse pattern at withdrawal is not governed in any way by sensory feedback from the eye; the pattern of motor impulses in the two axons is independent of whether the eye is free to move, already artificially pushed into its socket, clamped, or removed altogether. The pattern still emerges, in fact, from isolated brains, in which the activity of the larger of these two axons has been the subject of a special study (Sandeman, 1967).

The peculiar pattern of muscles which actually bring about withdrawal emphasizes once more that individual eyecup muscles cannot be considered in isolation. Each muscle may have a particular effect in moving the eyecup if it alone is active, but in normal activity many muscles are active at all times and any new movement involves several muscles. It should not be thought peculiar that muscle 21 is active during

withdrawal *away* from the mid line, when normally it pulls the eye *towards* the mid line. The joint is broad while the muscles are short, so that a muscle may be at opposite sides of the pivot point in different parts of the traverse of the eyecup. In addition the position of the pivot changes during the movement (Burrows & Horridge, 1968*a*). Moreover it is impossible to demonstrate that the peculiar innervation pattern by the two axons to seven muscles is the mechanical optimum; it may be no more significant than an adequate pattern which can conveniently develop.

SUMMARY

1. Protective withdrawal of the eyecup is caused by a burst of impulses in two axons of the optic tract, one to muscles 19a, 19b and 20a, the other to muscles 18, 20b, 21 and 22.

2. At a reflex eyecup withdrawal other concurrent activity is mechanically overridden; the tonic activity in only one muscle is inhibited centrally. At a 'spontaneous' withdrawal, however, all motor activity to that eyecup is inhibited.

3. The largest muscle, 19a, inactive in other eyecup movements, is the prime mover in withdrawal, and some tonic fibres of this muscle hold the eyecup withdrawn.

4. Two muscles which move the eyecup toward the mid line on optokinetic responses are excited during a withdrawal. It is therefore possible for one muscle to contribute to movements in opposite directions.

5. Repeated reflex withdrawal of an eyecup moving towards the mid line inhibits the optokinetic response of the other eye.

6. Weak stimulation of an eyecup region by a variety of means, including withdrawal, improves the optokinetic response of that eyecup and sometimes of the other eyecup

REFERENCES

BETHE, A. (1897). Das Nervensystem von *Carcinus maenas*. Ein anatomisch-physiologischer Versuch. 1. Theil. 1. Mittheilung. *Arch. mikrosk. Anat.* **50**, 460–546.

BURROWS, M. (1967). Reflex withdrawal of the eyecup in the crab *Carcinus*. *Nature, Lond.* **215**, 56–7.

BURROWS, M. & HORRIDGE, G. A. (1968*a*). The action of the eyecup muscles of the crab *Carcinus* during optokinetic movements. *J. exp. Biol.* **49**, 223–50.

BURROWS, M. & HORRIDGE, G. A. (1968*b*). Motoneurone discharges to the eyecup muscles of the crab *Carcinus*. *J. exp. Biol.* **49**, 251–67.

BUSH, B. M. H., WATERMAN, T. H. & WIERSMA, C. A. G. (1964). Efferent mechanoreceptive responses in the optic nerve of the crab *Podophthalmus*. *J. cell. comp. Physiol.* **64**, 327–46.

HORRIDGE, G. A. (1966*a*). Optokinetic memory in the crab, *Carcinus*. *J. exp. Biol.* **44**, 233–45.

HORRIDGE, G. A. (1966*b*). Adaptation and other phenomena in the optokinetic response of the crab *Carcinus*. *J. exp. Biol.* **44**, 285–95.

HORRIDGE, G. A. & SANDEMAN, D. C. (1964). Nervous control of the optokinetic responses in the crab *Carcinus*. *Proc. R. Soc.* B **161**, 216–46.

SANDEMAN, D. C. (1964). Functional distinction between oculomotor and optic nerves in *Carcinus* (Crustacea). *Nature, Lond.* **201**, 302–3.

SANDEMAN, D. C. (1967). Excitation and inhibition of the reflex eye withdrawal of the crab, *Carcinus*. *J. exp. Biol.* **46**, 475–85.